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POSTGLACIAL BIOGEOGRAPHY

AND THE DISTRIBUTION OF *POANES VIATOR* (HESPERIIDAE) AND OTHER MARSH BUTTERFLIES

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THE DISTRIBUTIONS OF MANY NORTH AMERICAN BUTTERFLIES and skippers are poorly known. In the course of a study of the biology of the Broad-Winged Skipper, *Poanes viator* (Edwards), it became clear that all published statements of the range were incorrect or inadequate; moreover, the actual distribution revealed by assembled data from collections, private collectors, and published sources was of a peculiar type virtually unreported for animals but well known for many years to botanists: the "Atlantic Coastal Plain-Great Lakes" disjunction. The ranges of several other poorly known species were then examined, and a repeating pattern emerged. This paper considers the nature and significance of that pattern.

THE RANGE OF *POANES VIATOR*

Edwards (1865) knew of only two localities for *P. viator*: northern Illinois and the vicinity of New Orleans. French (1885) gave "Gulf States, Massachusetts, New Jersey, Illinois, Wisconsin." Scudder (1889) showed it continuously distributed in the Mississippi Valley. Klots (1951) gave the range as:

> Massachusetts, southern Ontario, Minnesota, and Nebraska, south to Alabama and Texas; records scattered, not from all states within this general area. (p. 249)

The range figured (Fig. 1) is quite different. It includes four records which are queried. The single record at St. Louis (Knetzler, 1912) has not been confirmed by a specimen, and a veteran Missouri collector, Richard Heitzman, has never seen the species there. Forbes (1928) lists *P. viator* from Mount Marcy, New York, the highest peak in the Adirondacks—a seemingly unlikely habitat, and no specimen has been found.

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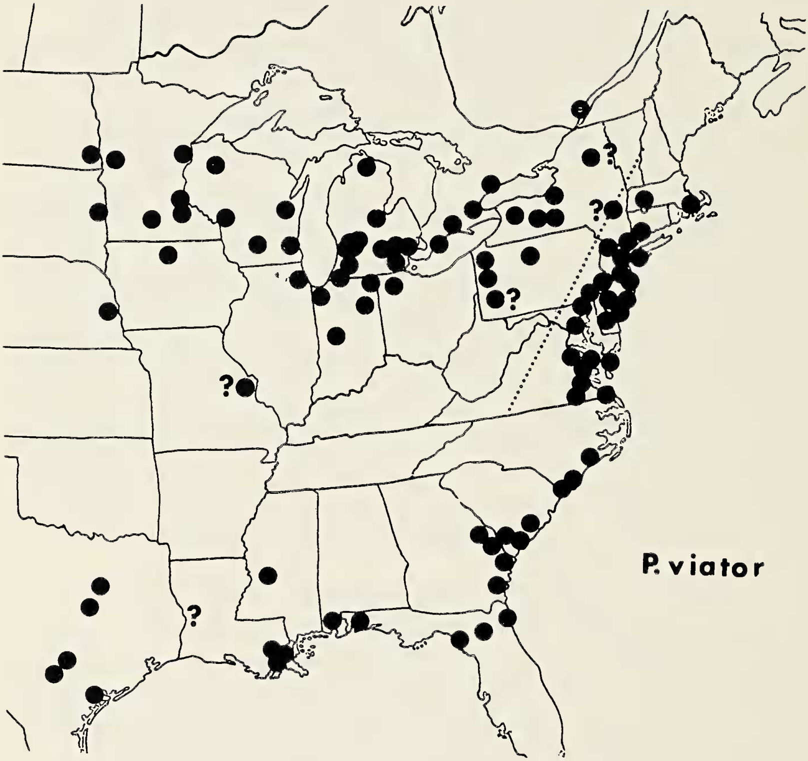

Fig. 1.—Distribution of *Poanes viator*. Dotted line shows western limits of *P. v. zizaniae*.

Chermock's record from Pittsburgh, Pa. (Tietz, 1952) is unverified, and there are no other southwestern Pennsylvania records. Bailey (1877) recorded *viator* from the sand plain at Karner, Albany County, New York. This is probably an accurate record, but no one has found the species since. It does not appear in the long series of Albany skippers at the New York State Museum, but many old specimens have been destroyed or discarded for lack of data. If a population once existed at Karner it was presumably the Coastal Plain subspecies, *P. v. zizaniae* Shapiro. One record omitted from the map is the Missouri Ozarks (Sell, 1916), given in a list including at least eight misdeterminations or falsifications.

The actual range thus divides neatly into the Coastal Plain element, *zizaniae*, from Massachusetts to Texas, and a Great Lakes element, nominate *viator*, from near Montreal to Nebraska and South Dakota. These two areas are separated by a narrow zone along the Appalachians in Pennsylvania and New York in which neither subspecies occurs. The same type of distribution in plants has led to repeated discussion of the origins of the "Coastal Plain element" in the Great Lakes flora (Peattie, 1922; McLaughlin, 1932; Cushing, 1965). Plant geographers usually interpret such disjunct distributions in terms of range changes following the last (Wisconsin) glaciation.

TYPES OF COASTAL PLAIN SPECIES

The Coastal Plain (Fig. 2) is clearly demarcated as a physiographic province by the character of the topography and the nature of the soils and underlying materials. At a given latitude, differences in vegetation occur across the Fall Line (cf. Hitchcock and Standley, 1919). Many species of plants and butterflies occur generally across the Fall Line, but other species may be considered of primarily Coastal Plain distribution. McLaughlin (1932) divided the plants into five groups, four of which are also represented among the butterflies:

1. Species and subspecies (other than salt marsh obligates) wholly restricted to the Coastal Plain: *Cercyonis pegala pegala* Fabricius, *Lethe portlandia portlandia* Fabricius, *Papilio palamedes* Drury, *P. troilus ilioneus* Abbot and Smith, *P. glaucus australis* Maynard, *Mitoura hesseli* Rawson and Ziegler.

2. Coastal Plain species and subspecies which also occur more or less frequently northward and westward, but generally near the Fall Line (the restriction becoming more severe north-

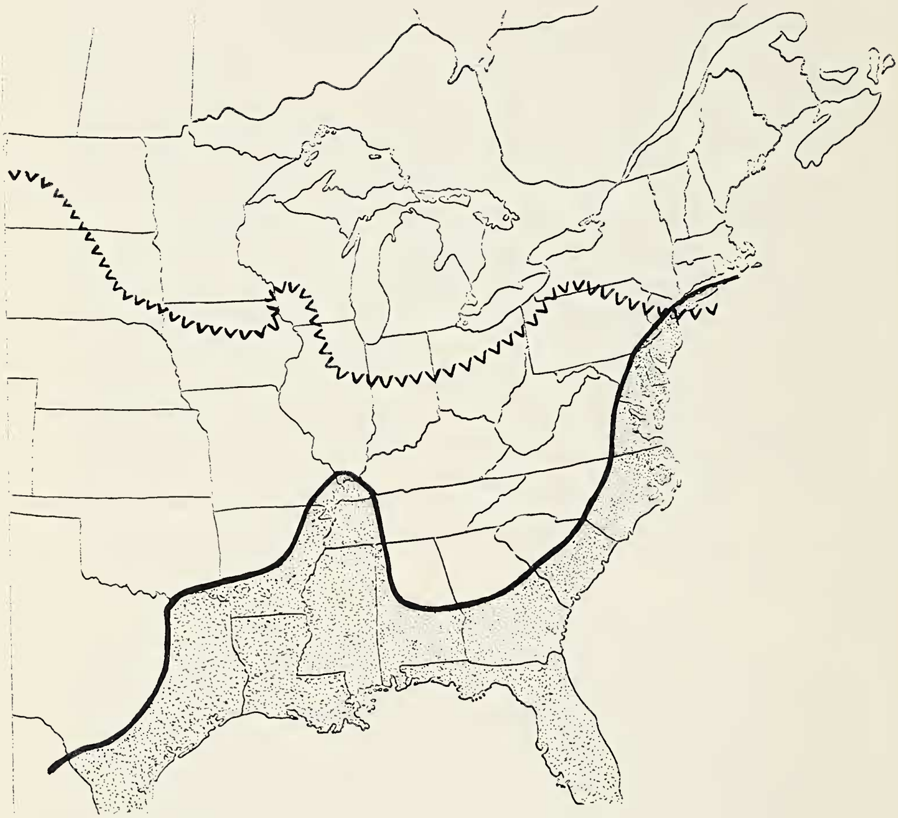

Fig. 2.—The Atlantic Coastal Plain (stippled) and the southern limits of the Wisconsin glaciation.

ward): *Euptychia areolata* Abbot and Smith, *E. hermes sosybia* Fabricius, *Phyciodes phaon* Edwards, *Erynnis horatius* Scudder and Burgess, *Wallengrenia otho* Abbot and Smith, and (as migrants) *Precis coenia* Hubner and *Phoebis sennae eubule* Linnaeus.

3. Widespread northern species penetrating southward farther on the Coastal Plain than inland: *Incisalia augustinus* Westwood, *I. polios* Cook and Watson, *Lycaena epixanthe* Boisduval and Le Conte, and the (genetically determined) *"lucia"* form of *Lycaenopsis pseudargiolus* Boisduval and Le Conte.

4. Species occurring more or less generally on the Coastal Plain, and disjunctly around the Great Lakes: *Poanes viator, P. massasoit* Scudder, *Euphyes dion* Edwards, *E. conspicua* Edwards. *E. dukesi* Lindsey, *Euptychia mitchellii* French, and *Pyrgus communis* Grote.

5. Coastal Plain species with close relatives endemic in the Great Lakes region. We have no butterfly species pairs strictly fitting this category, but the pairs *Euptychia areolata-E. mitchellii* and *Euphyes dion-E. alabamae* Lindsey are related to it; see below.

Differences in the extent to which Coastal Plain species and subspecies are distributed inland depend on two factors: suitability of inland areas for successful colonization and the ability of the species to reach them, both by short-term dispersal and long-term range changes. Cushing (1965) has rightly noted that that the range of each species is the result of its own unique history and biological properties. Treating species with superficially similar ranges as a unit with a common history may obscure important differences among them. Some of the Coastal Plain obligates, such as *Mitoura hesseli,* are obviously limited by the distributions of their food plants; others are not. The species in categories 3 and 4 above both seem to form ecologically defined units. At least three of the four species in category 3 are Ericaceous feeders and their distribution reflects the extent of acid barrens and bogs on the Coastal Plain.

All of the species in category 4 except *Pyrgus communis* are limited to marshes, feed on sedges (Cyperaceae) or (some populations) grasses (Gramineae), and, at least northward, are univoltine in midsummer. As will be shown below, all of the other eastern North American butterflies (except Florida endemics and the subarctic Satyrids) with these same characteristics have distributions closely related to the Coastal Plain-Great Lakes one, while few other species do. Moreover, these

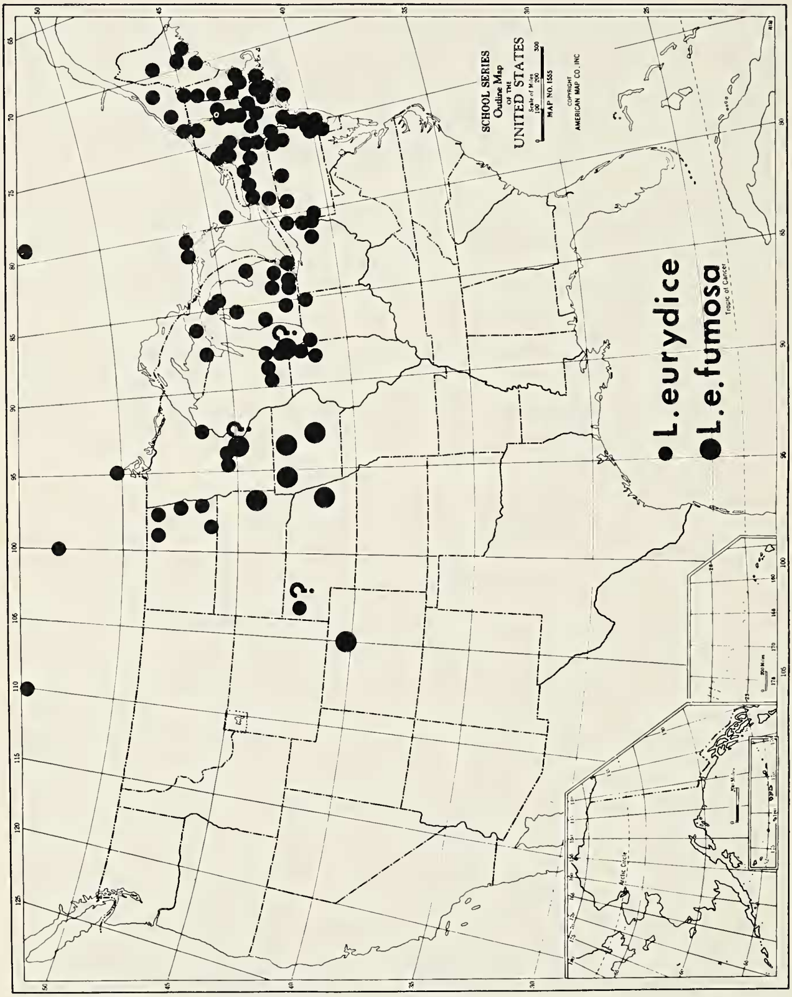

Fig. 3.—Distribution of *Lethe eurydice* subspecies.

six species all tend to be highly localized, and are not active colonizers today; their low vagility and the relative inaccessibility of their habitats make recent range extensions through human interference unlikely. The historical basis for category 4 distributions is, however, much less obvious than that for category 3.

THE COASTAL PLAIN-GREAT LAKES RANGES

The ranges falling in or related to this category involve various combinations of three areas: the northern and Mid-Atlantic portion of the Coastal Plain, the Gulf portion and lower Mississippi Embayment, and the Great Lakes region. They also entail various degrees of differentiation among the component populations.

Great Lakes-Northern Coastal Plain, nondisjunct. — *Lethe e. eurydice* Johansson (Fig. 3) is an example of a butterfly whose range extends continuously across the northeastern quarter of the United States, with no break in New York and (northern) Pennsylvania. It is a univoltine, *Carex*-feeding marsh species (Shapiro and Cardé 1970; Cardé, Shapiro, and Clench, 1970).

Great Lakes - Northern Coastal Plain, nondisjunct; southern Coastal Plain, disjunct. — The ranges of *Euphyes bimacula* Grote and Robinson (Fig. 4) might be considered similar to *L. eurydice* and likely to have a similar history, except for the two (widely separated) disjunct colonies far to the south (discussed and confirmed by Mather and Mather, 1958) and a specimen form Southern Pines, N.C., in the U.S. National Museum.

Great Lakes-Northern Coastal Plain, disjunct. — Superficially the range of *Euphyes conspicua* (Fig. 5) resembles that of *L. eurydice,* but it breaks in New York and Pennsylvania. I have visited many marshes in the critical area at the appropriate season without finding it. There are no phenotypic differences between eastern and western specimens, but Nebraska ones (*buchholzi* Ehrlich and Gilham) are larger and darker than others.

Poanes massasoit (Fig. 6) is nearly identical, except that a single isolated population occurs midway between the eastern and western ranges, in the Beaver Creek basin near McLean, New York (Shapiro, 1969, 1970a). Although the Lakes and Coastal Plain butterflies are virtually identical, Beaver Creek specimens differ consistently from them in phenotype (Fig. 7).

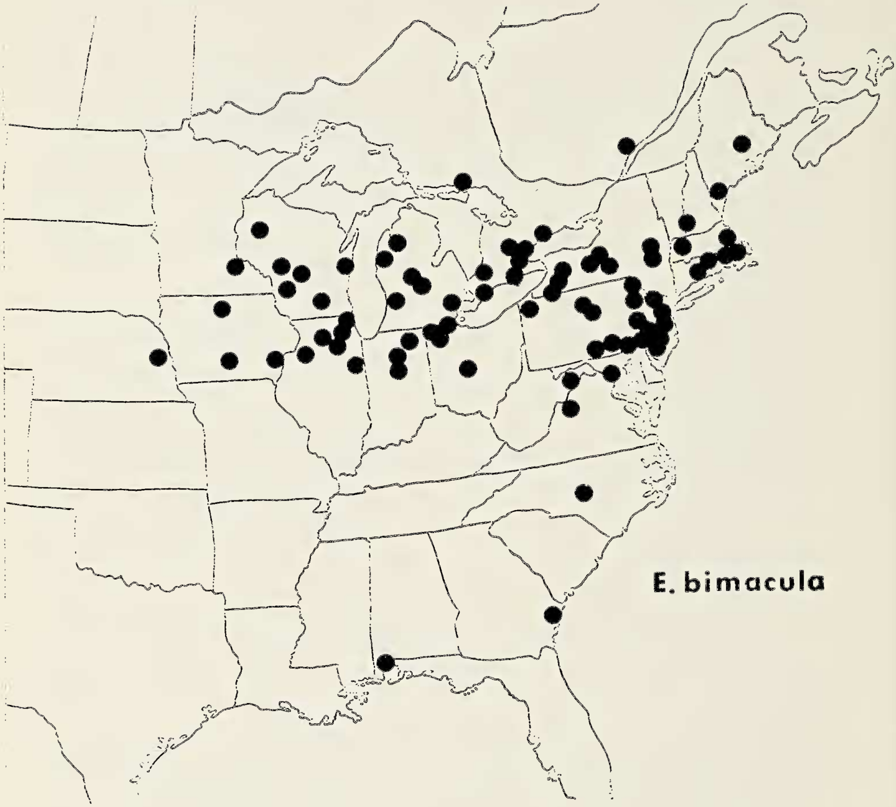

Fig. 4.—Distribution of *Euphyes bimacula*.

Great Lakes-entire Coastal Plain, disjunct. — The northern distribution of *Poanes viator* (Fig. 1) is almost identical to *E. conspicua,* but on the Coastal Plain it extends south and west to Texas. The populations are subspecifically differentiated. The grasshopper *Trimerotropis maritima* Harris has a similar distribution, except that its southern range does not extend west of west-central coastal Florida. The Lakes population extends from southern Ontario to southeastern Minnesota and northern Indiana, and is recognized as a subspecies (*interior* Walker). (See McNeill, 1902; Blatchley, 1920.)

Great Lakes-Northern Coastal Plain-Southern Coastal Plain, both disjunct. — *Euphyes dukesi* (Fig. 8) has the most extraordinary distribution of any North American butterfly, though the extremeness of its disjunctions has been lessened by the addition of data unknown to Mather (1963). The populations are not phenotypically differentiated.

Great Lakes-Northern Coastal Plain/Southern Coastal Plain, two species. — Mather (1965) noted that superimposing the Lake Michigan range of *Euptychia mitchellii* on a map of the closely related *E. areolata* gave a result reminiscent of the range of *Euphyes dukesi.* The recent rediscovery of *E. mitchellii* in New Jersey (Rutkowski, 1966) reinforces this impression; though the New Jersey colony is several miles above the Fall Line the relationship of this range to the others seems evident (Fig. 9). McAlpine, Hubbell, and Pliske (1960) suggested conspecificity of these two taxa.

Euphyes dion and *E. alabamae* (Fig. 10) present a similar case. Until recently considered conspecific, they are now known to be sympatric on the Coastal Plain from Maryland to South Carolina (recently reported from Florida by Clench, *in litt.*). I have been unable to find records, museum specimens, or colonies in the field to connect the central New York and Connecticut-New Jersey populations of *E. dion,* which are possibly slightly differentiated phenotypically.

POSTGLACIAL MIGRATION ROUTES AND CLIMATE

The very extensive literature on post-Wisconsin climate and biogeography can be summarized only very briefly here. Virtually all of the Great Lakes region was under ice at the Wisconsin maximum (Fig. 2). The ice sheets eradicated all plant and animal life in their paths, and displaced the biota southward in a basically zonal pattern complicated by geo-

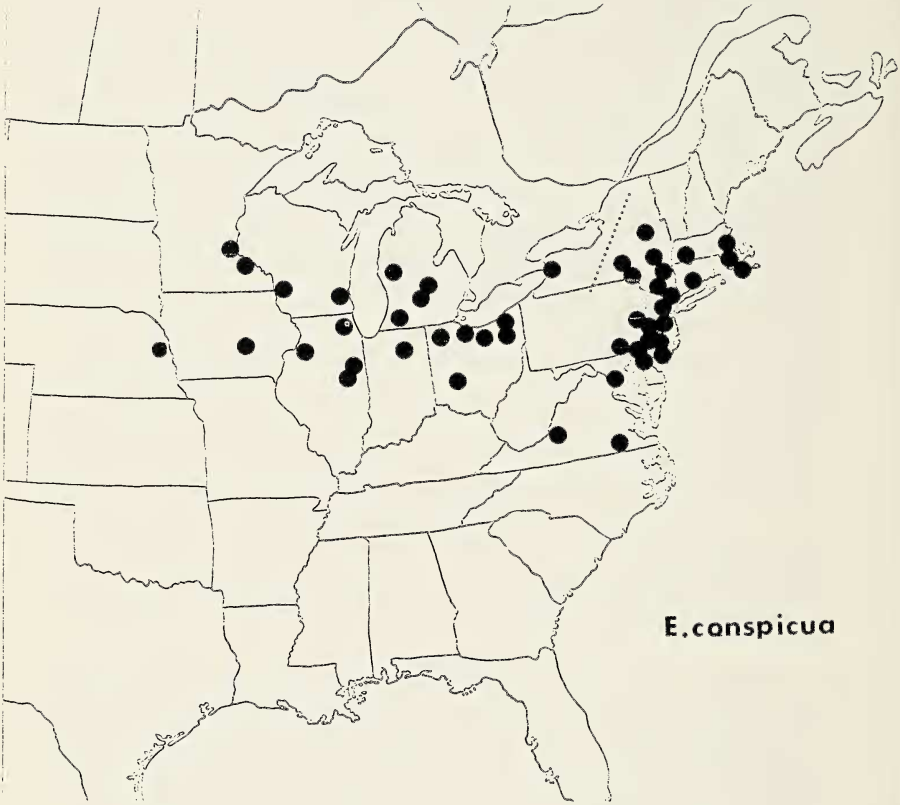

Fig. 5.—Distribution of *Euphyes conspicua*. Dotted line indicates disjunction in New York.

graphic factors and relict effects of earlier Pleistocene biotic migrations. After the ice retreated the biota returned northward. Our knowledge of post-Wisconsin climate and vegetation is largely inferred from pollen preserved in peat (Cushing, 1965; Davis, 1963, 1965). A fairly generally accepted chronology for post-Wisconsin climate in eastern and central North America, correlating well with that for western and central Europe, has emerged (cf. Cox, 1959; Cushing, 1965; Davis, 1965; Deevey, 1949; Dillon, 1956; Flint, 1947; Gleason, 1922; Smith, 1957; Terasmae, 1969). The disjunct ranges of our butterflies may be interpreted in terms of this chronology.

Euphyes bimacula affords clear evidence of the far southward displacement of northern species as a result of glaciation (not necessarily in the Wisconsin). The locations of the relict southern populations imply that a glacial refugium existed in the southeast. If modern populations were derived from those migrating northward from such a refugium, *E. bimacula* reached the Great Lakes *from the east*. How might it have done so?

As the glaciers retreated, they dammed up great amounts of water in the basins of the future Great Lakes. These bodies of water were drained as the region was uplifted by isostatic rebound behind the ice sheet (Taylor, 1915; King, 1965; Zoltai, 1969). While the St. Lawrence Valley was still blocked by ice, the Ontario basin discharged via the Mohawk Valley to the Hudson and thence to the Atlantic (Hough, 1958). The Hudson-Mohawk outlet probably existed between 12,500-10,500 B.P., providing a route for Coastal Plain organisms to reach the Great Lakes. Associated with the outlet, a nearly continuous band of marsh vegetation would have provided a corridor across New York State for the category 4 butterflies and others to colonize areas farther west. The opening of the St. Lawrence lowered the level of Lake Ontario, drying up the Mohawk Valley. Many of the populations of species now disjunct in New York may have become extinct at that time.

Euphyes bimacula and *Poanes viator* very probably followed this route from east to west; although *Poanes massasoit* and *Euphyes conspicua* have no southeastern populations today, they are also easily included in the model. The genus *Euphyes* is strongly eastern, with three endemic species in Florida and only one (the very wide-ranging *E. ruricola metacomet*, an old-field grass feeder) in the lower Mississippi Valley. *Poanes* is similarly eastern.

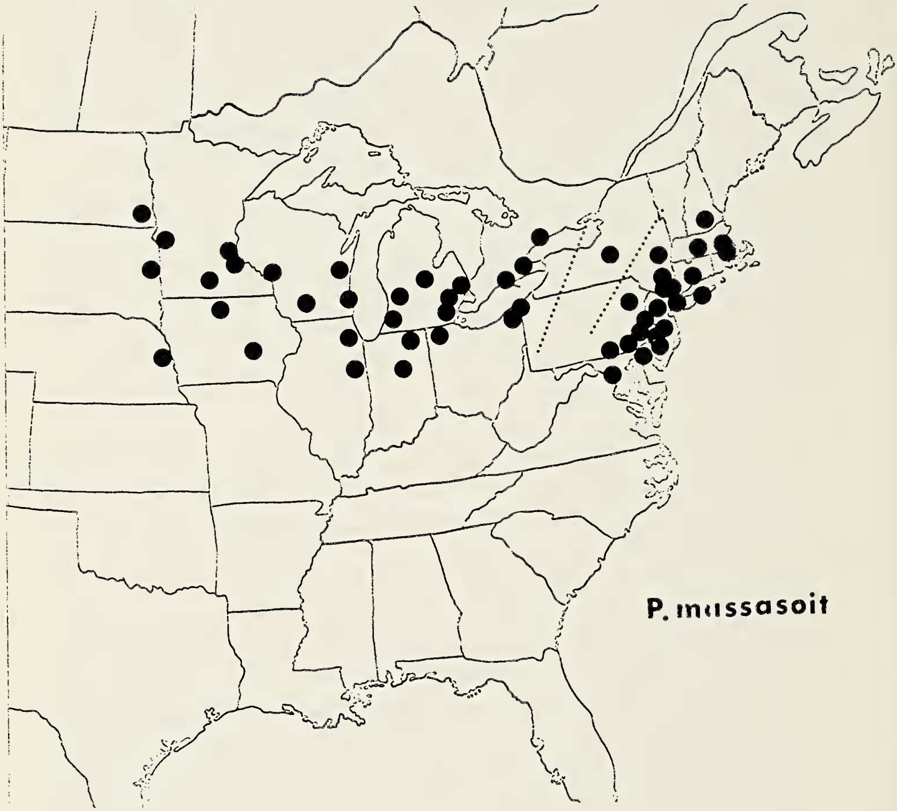

Fig. 6.—Distribution of *Poanes massasoit.* Dotted lines indicate area in which only one population (Beaver Creek) is known.

While the drainage pattern of the Great Lakes was changing, the climate warmed rapidly to a "climatic optimum" during which mesophytes such as elm, beech and hemlock displaced the spruce and pine which had followed the glaciers. About 5000 B.P., as reflected by a marked decline of hemlock in pollen profiles and a corresponding increase in oak, the climate began to dry and more xeric vegetation spread eastward, permitting western elements to enter the northeastern biota. Smith (1957) presents distributional evidence from reptiles and amphibians indicating penetration of western elements to the Altantic Coastal Plain in the DelMarVa peninsula. *Plebeius melissa samuelis* Nabokov (Fig. 11) presumably spread east at this time, reaching New England. About 2500 B.P. the climate was becoming cooler and more humid as it is today, and species which had invaded the northeast during the xerothermic interval declined as the mesic biota reasserted itself. Xerothermic relicts were left where soil or other local conditions permitted them to persist; *P. m. samuelis* is restricted to sandy soils (Shapiro, 1969). Cooler temperatures than prevailed before the xerothermic interval may have limited the dispersal of some of the mesic species.

Pollen profiles for several central and southern New York bogs show the xerothermic interval clearly as an oak-beech maximum and a very marked hemlock minimum (Cox, 1959). Cox and Lewis (1965) found a strong oak-hickory maximum in the profile for Crusoe Lake in central New York. This dry interval may have contributed to the extinction of remaining populations of marsh butterflies with disjunct modern distributions. The Beaver Creek colony of *P. massasoit* is in a basin which has undergone continuous bog development since the recession of the ice sheet (Cornell University, 1926; Cox, 1959).

An alternative hypothesis to the westward spread of Coastal Plain species to the Great Lakes is that they migrated northward up the Mississippi Valley, spreading from *west to east* into New York. This is probably true of *Lethe eurydice* (Cardé, Shapiro, and Clench, 1970). Some species might have moved northward via both routes, either merging in the northeast or never coming into contact, leaving the disjunction observed today.

McLaughlin (1932) shows that very few of the Coastal Plain-Great Lakes plants followed the Mississippi Valley route, but his explanation of this (that changes in course and climatic instability made the Mississippi floodplain at best an uncertain

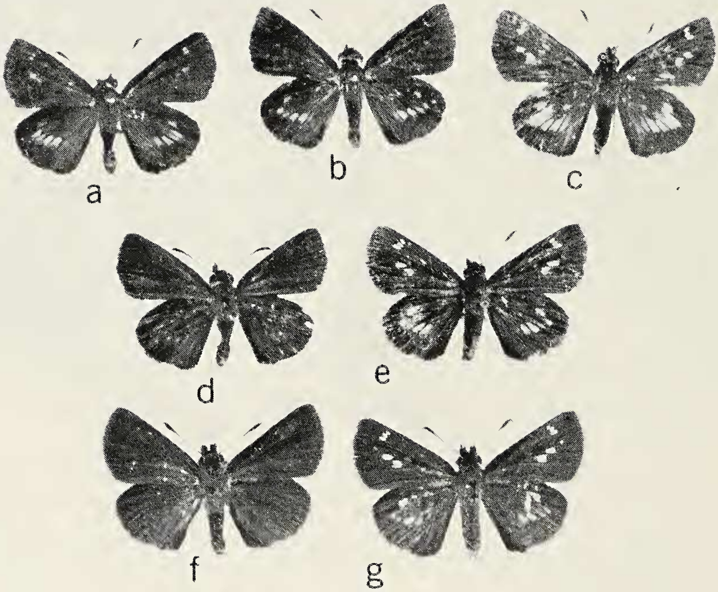

Fig. 7.—*Poanes massasoit*. a-c: Beaver Creek basin, Tompkins County, N.Y., vii.23.68 (a, b, ♂; c, ♀). d (♂) and e (♀): Rockland County, N.Y., vii.20.68. f (♂) and g (♀): Burlington County, N.J., 1964.

corridor) seems weak. Whatever the reason, there are no relict populations in the Mississippi Valley or the Ozarks to support this hypothesis for most of our butterflies. Even with the new Illinois data, *Euphyes dukesi* remains an ambiguous case and could have spread northward by either or both routes. *Problema byssus* Edwards (Fig. 12) clearly spread northward up the Mississippi Valley, but never reached the Great Lakes.

TWO ANOMALOUS RANGES

Hesperia metea Scudder (Fig. 13) seems to have migrated northward in both the Coastal Plain and the Mississippi Valley, but where did the seemingly isolated Michigan-Wisconsin population come from? This species occurs primarily in open sandy barrens in the northeast (Shapiro, 1965) and in open pine-oak woodland to the south and southeast, and would seem a likely candidate for east-west dispersal in the xerothermic. Yet there are apparently no populations between Tioga County, New York and Michigan. Several hypotheses can be constructed to account for this, but none is satisfactory given the amount of data at hand. The very short flight season makes it likely that the range of this species is still poorly known.

The Regal Fritillary, *Speyeria idalia* Drury (Fig. 14), shows a number of range anomalies. It is abundant on the prairies in Kansas and Nebraska in some years and also occurs in the Ozarks. Its distribution seems continuous along the south shore of Lake Erie, suggesting an eastward spread during the xerothermic interval. However, it extends south in the Appalachians at least to North Carolina, raising serious doubts as to whether the northeastern populations could have come from the west alone. Rather than spreading south in the mountains after the xerothermic, *idalia* may well have spread north in both the east and the west, becoming confined to higher elevations in the lower Appalachians as the climate warmed. The two northward advances would then have met in Pennsylvania or New York, if at all. *S. idalia* is conspicuously absent from the Finger Lakes and Mohawk Valley in central New York, though it extends up the Susquehanna drainage to Binghamton and also exists in the southwestern part of the state. It is possible that these populations are not in contact today and even that the western *idalia* never penetrated further into the northeast than southwestern New York.

S. idalia also occurs disjunctly in the eastern foothills of the Colorado Rockies. Like *Lethe eurydice fumosa* Leussler (dis-

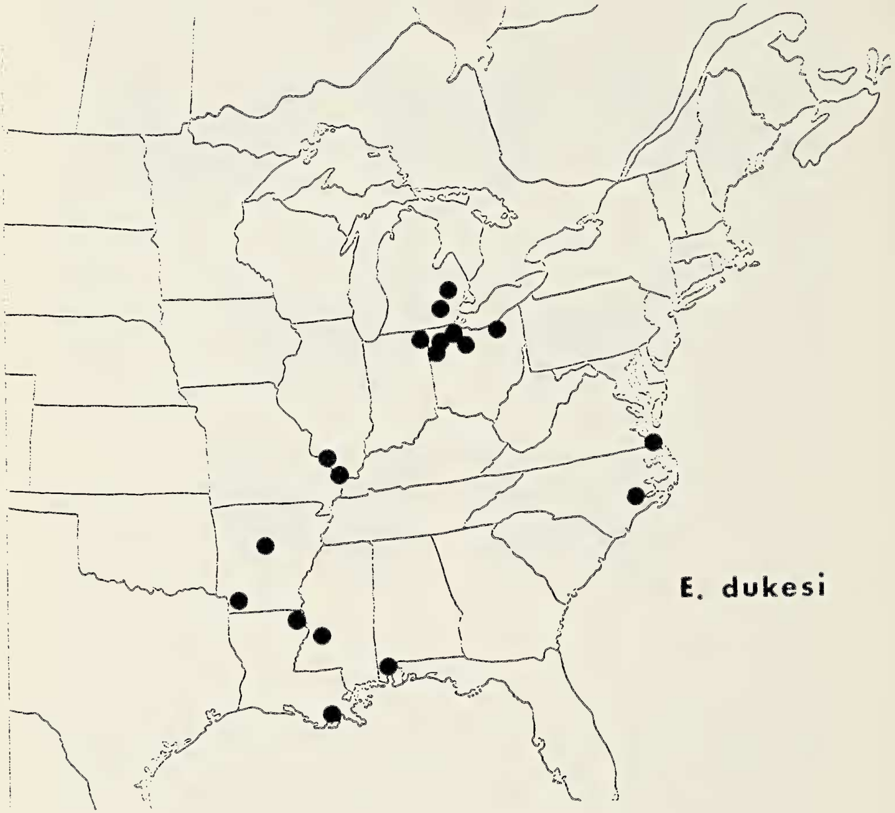

Fig. 8.—Distribution of *Euphyes dukesi*.

cussed below), it probably reached there during the climatic optimum and was stranded there when the western plains became appreciably drier at roughly the same time as S. *idalia* was spreading northeastward in the Ohio-Lake Erie area.

GENETIC DIFFERENTIATION

If the subspecific differences in *Poanes viator* arose after the closing of the Mohawk outlet, they have had some 10,000 generations in which to come about. The same can be said for the differentiation of the Beaver Creek population of *Poanes massasoit.* In this case, however, the entire modern population probably does not exceed 200 individuals in most years, and may be much less. The population is thus susceptible to rapid change by either natural selection or genetic drift.

None of the species pairs can be dated with any certainty. The distribution of *Problema* (Fig. 12) suggests at least two periods of isolation in Florida, one of which gave rise to *P. bulenta* Boisduval and LeConte. The isolated Florida *Hesperia metea* also probably represent a prior refugium, perhaps cut off at a time when Florida was an island. Isolation during the Pleistocene may have contributed to the origin of *Lethe eurydice fumosa,* the range of which consists today of widely disjunct colonies from Colorado to Iowa (Fig. 3).

The disjunct occurrence of *L. e. fumosa* in Colorado is duplicated in *Erynnis martialis* Scudder, a species otherwise very differently distributed (Fig. 15, modified from Burns, 1964). *E. martialis* also occurs disjunctly in the Black Hills of South Dakota, also probably as a relict of its pre-xerothermic distribution. The northern limits in the plains today are in the bottomlands of the Missouri and Mississippi Rivers. *E. martialis* seems to have taken both the eastern and western routes northward. Its populations in central New York (Tompkins, Schuyler, Cayuga, Yates Counties) may be disjunct from those in the Hudson Valley and Albany County; if so it and *Pyrgus communis* (discussed below) would be the only non-marsh skippers to show this pattern. There is no phenotypic differentiation evident among the various populations of *E. martialis,* but contrary to the statements of Burns (1964), it is univoltine at least in central New York.

TWO MULTIPLE-RELICT AREAS

The Omaha, Nebraska area seems to have been a xerothermic refugium for at least six butterfly species, two of which (*Boloria selene nebraskensis* Holland and *Euphyes conspicua bucholzi*)

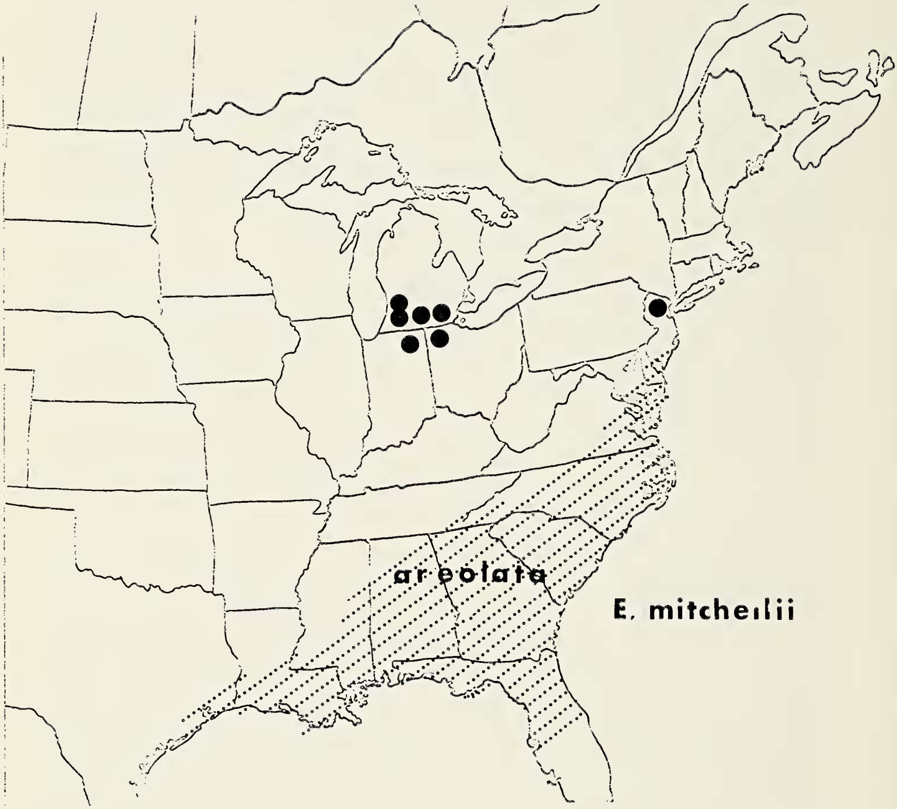

Fig. 9.—Distribution of *Euptychia areolata* and *E. mitchellii.*

developed distinctive endemic forms there. Nebraska *Poanes v. viator* are larger and brighter than other populations of that subspecies, but no information is at hand on their biology. The other three relict species are *Euphyes bimacula, Poanes massasoit* and *Lethe eurydice fumosa.*

The Omaha area was well suited as a refugium because of its ravines and valleys, deepened in Wisconsin time and later partly filled with alluvium on which marshes developed (Reed *et al.,* 1965). If this explanation of the relicts is correct, they must have reached Nebraska from the north and east (except perhaps *L. e. fumosa*?) before the xerothermic maximum. *Erynnis horatius* and *E. martialis* reach their northernmost plains stations near Omaha today (Burns, 1964) in bottomland forest; these do not appear to be relict occurrences.

Another noteworthy multiple-relict area for butterflies is the Great Dismal Swamp on the Coastal Plain at the North Carolina-Virginia border. Clark and Clark (1951) list from there the following "upland" species: *Lethe appalachia* Chermock, *Euphyes conspicua, Poanes hobomok* Harris, and *Speyeria diana* Cramer. Pollen data for the Swamp (Whitehead, 1965) do not help to explain this disjunct faunal component, although the full-glacial vegetation was more "northern" than today. The Clarks were of the opinion that intervening populations on the Piedmont, connecting those in the mountains and the Dismal Swamp, had been exterminated by man.

THE RANGE OF *PYRGUS COMMUNIS*

The distribution and biology of the common Checkered Skipper are especially instructive in underlining the problems of inference from contemporary butterfly ranges. This is a vagile insect and an active colonizer of ruderal and old-field habitats, wherever its food plants (weedy Malvaceae, especially *Malva*) grow. Its populations probably correspond in structure to Wright's "neighborhood" model (Wright, 1951). It is one of the most widely distributed butterflies in North America, and is found throughout the east except in eastern New York and Pennsylvania and most of New England (Fig. 16). There is a marked disjunction through the same area as those of the marsh butterflies discussed earlier.

P. communis seems to have come northward behind the ice on both sides of the Appalachians, and its distribution is continuous across them south of Virginia. It is abundant in much of the Great Lakes region and extends east across southern

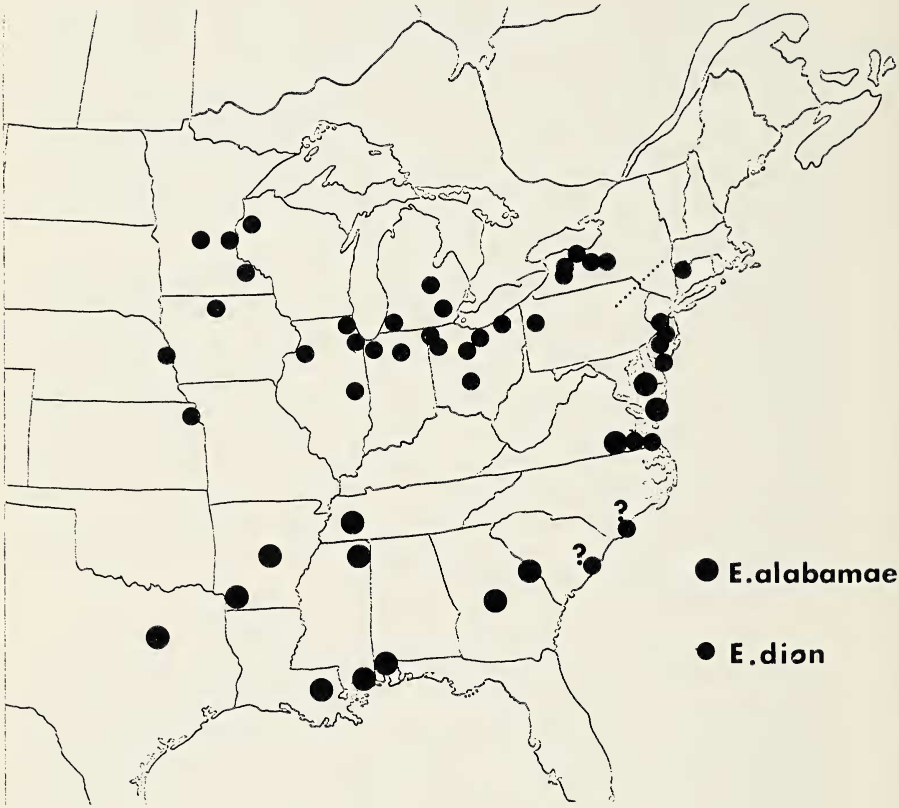

Fig. 10.—Distribution of *Euphyes dion* and *E. alabamae*. Note disjunction in eastern New York.

Ontario and the western half of New York. At least the New York range is recent, perhaps abetted by man. The first Ithaca specimens were taken about 1900; the first Erie County record is 1910 (Forbes, 1928). At Ithaca *P. communis* overwinters every year and has a large late spring flight. This seems to be duplicated throughout its upstate New York range, despite the severe winters. On the Coastal Plain the situation is very different; *P. communis* does not overwinter regularly anywhere north of Philadelphia, and even there stops at the Fall Line (Shapiro, 1966). The Connecticut and Massachusetts records are based on rare casuals, and the insect seldom overwinters at New York City (Davis, 1910; Forbes, 1928; Beutenmuller, 1902). At Philadelphia it seems clear that the distribution of *P. communis* is climatically limited. The western New York population does not appear to be spreading any further eastward; the same factors which limit the northward spread from the Coastal Plain may be limiting it as well. But it is also possible that the eastern and western insects are genetically differentiated with respect to overwintering ability, an hypothesis which could be tested by an introduction. There are no gross life history differences between the two stocks. The male genitalia of *P. communis* are very variable, showing more variation among individuals from the same date and locality than is found among species in many butterfly genera. No pattern of variation correlated with geography has been found.

Whatever the reason for its eastern New York disjunction, *P. communis* demonstrates that superficially similar distributions need not be related at all. There is nothing in its history or biology to suggest any community of interpretation with the marsh species.

The range of the introduced European Skipper, *Thymelicus lineola* Ochs., in North America as figured by Burns (1966) might suggest a climatic basis for disjunctions across central New York and Pennsylvania. In this case, however, it is known that somehow the insect "jumped" from the Lakes region to the Piedmont in Pennsylvania about 1952, and New Jersey about 1957. The gap between these expanding populations has been closed since 1967, and *lineola* now occupies all of central and western New York and also occurs in northeastern Pennsylvania (Shapiro, unpublished).

CONCLUSION

Historical biogeography is necessarily highly speculative.

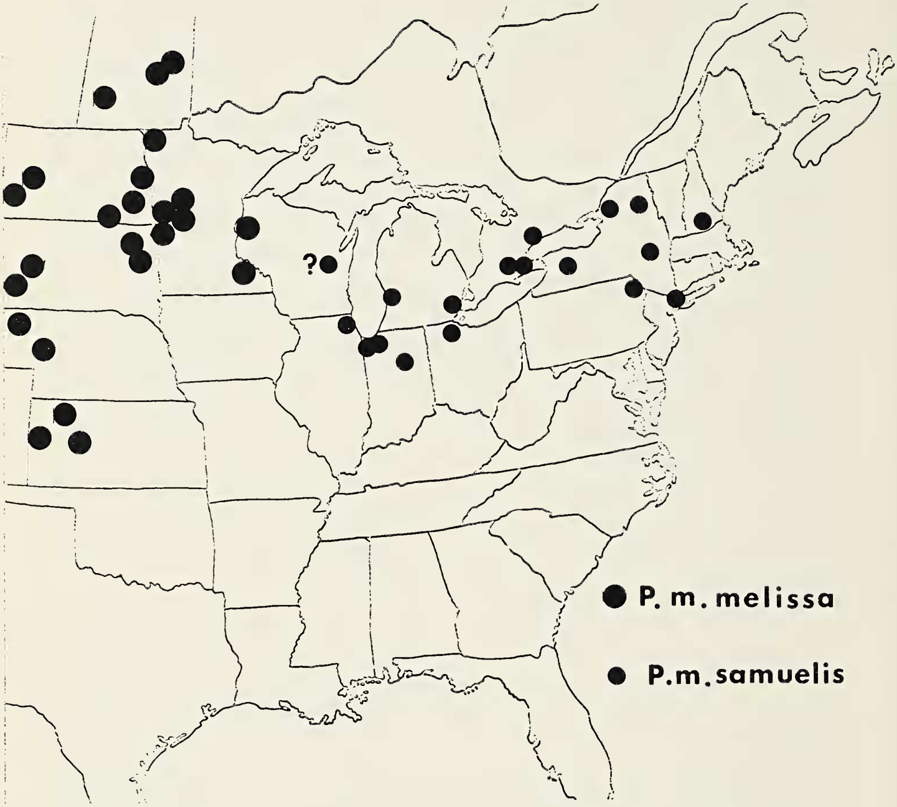

Fig. 11.—Distribution of *Plebeius melissa samuelis* and the eastern range of *P. m. melissa.*

This is even truer for butterflies, which in general leave no fossils, than for plants, which do. There is no butterfly equivalent of pollen profiles. Nonetheless, butterflies are so broadly dependent on plants that they would be expected to have followed them in their glacial and postglacial range changes. Interpretations of butterfly distributions must rely heavily on biogeographic evidence from other groups. They are also hampered by the difficulty in assembling large bodies of reliable data. Munroe (1969) has examined the ranges of some of the butterflies of Ontario. As he notes, both extensive surveys and intensive local studies are still revealing unexpected distributional information even in supposedly well-worked areas. Such new information may well require the re-evaluation of many of the ranges discussed in this paper.

Still, certain consistencies have appeared. There are about 450 species of butterflies recorded from North America east of the plains (Klots, 1951), of which about 130 each occur in New York (Forbes, 1928) and Pennsylvania (Shapiro, 1966; Tietz, 1952). Only seven species show a clear-cut Great Lakes-Coastal Plain range disjunction; all but one of these (which differs from the others in recent history as well as in biology) are marsh sedge feeders, and they make up a very large proportion of the eastern marsh butterflies. All of the remaining marsh sedge feeders (except salt marsh species, Florida endemics, and the subarctic Satyrids) show distributions related to the Great Lakes-Coastal Plain pattern. The common element in all these ranges seems to have been reliance on the post-Wisconsin Hudson-Mohawk outlet of Lake Ontario as a corridor connecting the Great Lakes and the Coastal Plain. The critical evidence needed to refute this hypothesis for a given species would be the existence of relict populations in the Mississippi Valley. For species with a break in New York and Pennsylvania, this would suggest that the Great Lakes populations were derived by migration from the southwest or south rather than the east, and that the gap in the range was analogous to that in *Pyrgus communis* —reflecting failure of two northward-moving populations to meet, rather than the extinction of previously connecting populations.

SUMMARY

1. Sedge-feeding marsh butterflies in eastern North America tend to be distributed in some variant of a basic Coastal Plain-Great Lakes pattern, often involving a break across

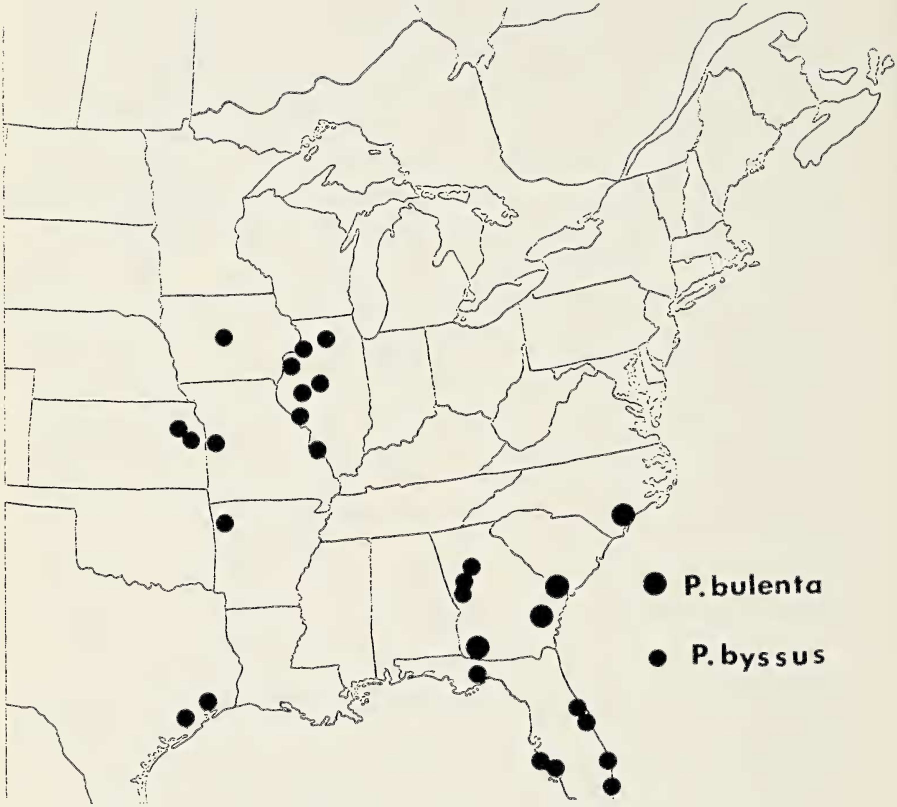

Fig. 12.—Distribution of *Problema byssus* and *P. bulenta.*

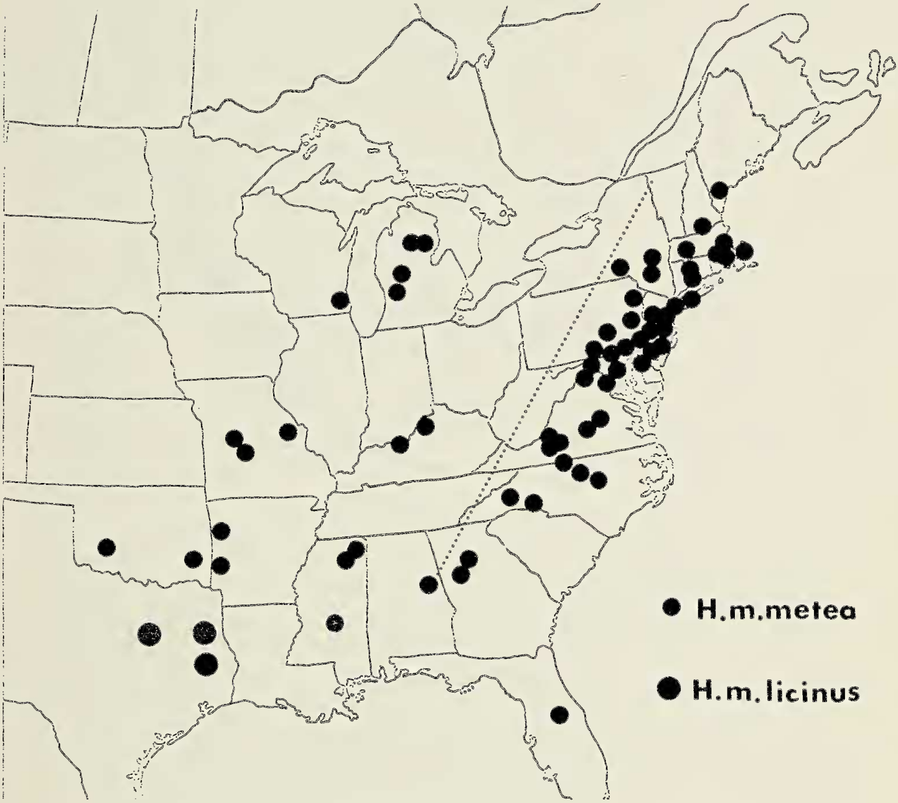

Fig. 13.—Distribution of *Hesperia metea.*

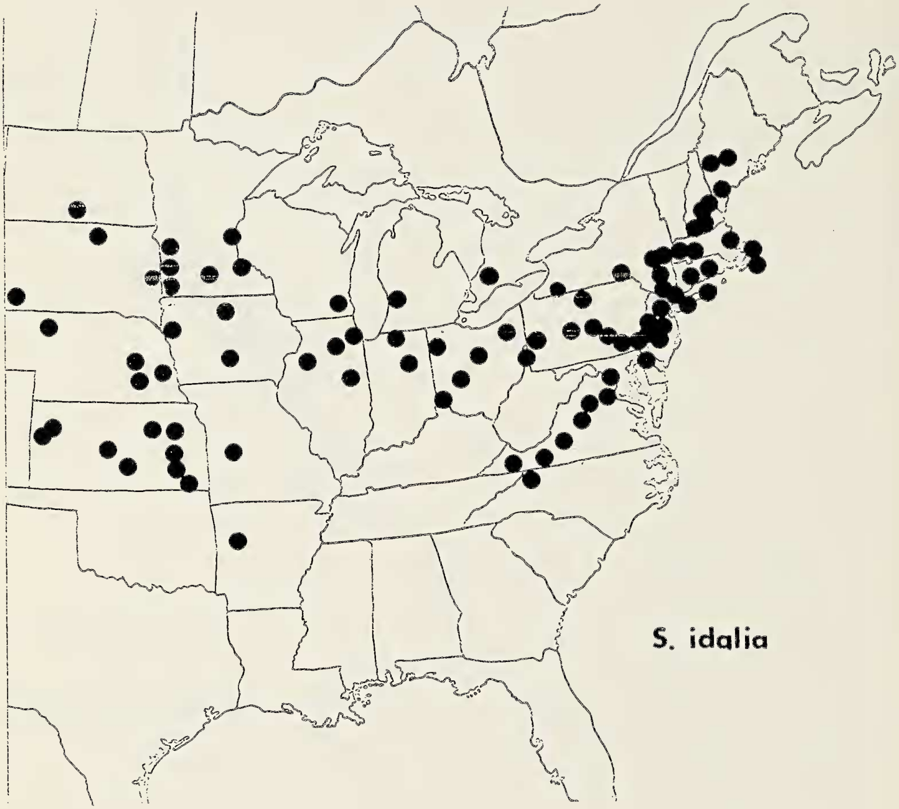

Fig. 14.—Distribution of *Speyeria idalia.*

New York and Pennsylvania. This type of distribution is rare in butterflies with different ecologies.

2. The prior existence of the Hudson-Mohawk outlet of Lake Ontario provides a hypothetical corridor for the migration of marsh species between the Coastal Plain and the Great Lakes. The isolated Beaver Creek population of *Poanes massasoit* confirms the prior existence of that species in an area of apparent range disjunction.
3. Evidence is presented which suggests that non-marsh, non-sedge feeding species with possible disjunctions in New York and Pennsylvania migrated northward after the Pleistocene both east and west of the Appalachians. These populations may have failed to meet in the northeast.

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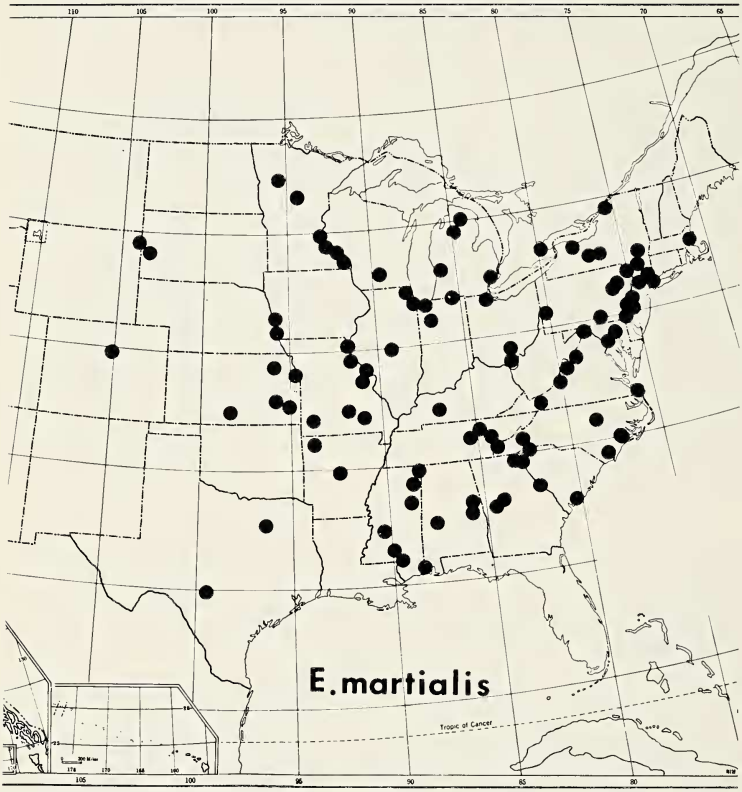

Fig. 15.—Distribution of *Erynnis martialis.*

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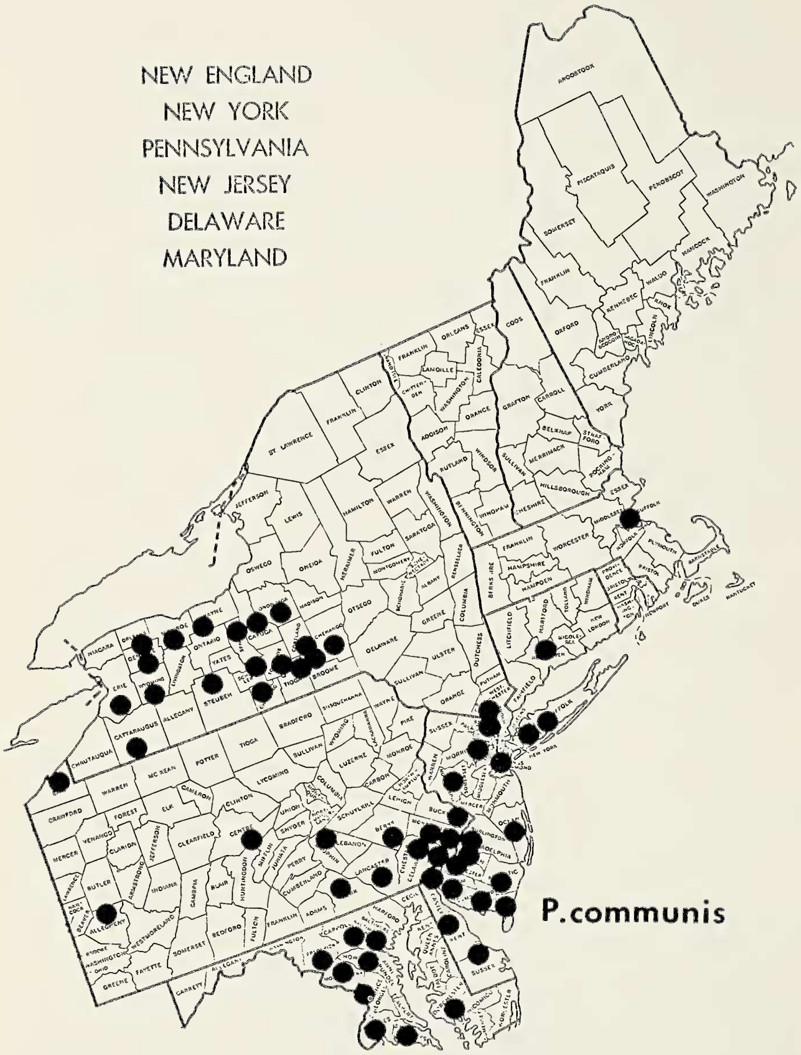

Fig. 16.—Northeastern U.S. distribution of *Pyrgus communis.*

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